

Chapter 2. Feeding, Prey Fields and Potential Competition of Young-of-the-Year Walleye Pollock (*Theragra chalcogramma*) and Pacific Herring (*Clupea harengus*) in Prince William Sound, Alaska in Summer and Autumn

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Abstract - Chapter 2

Diets of young-of-the-year (YOY) walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasii*) were compared between summer, early autumn and late autumn seasons and between autumn allopatric and sympatric fish aggregations in Prince William Sound (PWS), Alaska. Stomach samples were collected principally by mid-water trawl in the northeastern, central and southwestern regions of the sound during July 20-August 12, 1995, October 5-14, 1995 and November 7-13, 1994. Zooplankton samples were collected concurrently in vertical tows (303 μm mesh in summer and 243 μm mesh in early autumn) to characterize seasonal changes in prey fields and to assess prey selection.

Diets of YOY pollock and herring were principally composed of small calanoids in summer and of large calanoids, larvaceans and euphausiids in autumn. The seasonal diet shift to larger prey coincided with larger fish size and with decreased abundance and proportions of the principal zooplankton, small calanoids, and increased abundance and proportions of large calanoids and larvaceans in zooplankton tows. This change in prey was accompanied by trends toward decreased feeding in autumn compared to summer. All measures of food quantity declined for herring from early to late autumn and %BW declined for pollock from summer to late autumn. Herring and pollock in summer allopatric aggregations exhibited a high degree of diet overlap ($R_o > 0.76$). Diet overlap between sympatric species was higher and more consistent in late autumn ($R_o \leq 0.94$) than in early autumn ($R_o \leq 0.69$), when the quantity of food consumed was significantly greater (ANOVA, $p < 0.05$) for both species. Differences in prey selection between allopatric and sympatric herring could have been related to sampling time, depth or diel feeding rhythms, but could not be attributed to size or sympatry alone. The similarity in diets of both allopatric and sympatric YOY pollock and herring, which are important in commercial fisheries and as forage for marine birds and mammals, indicate potential for competitive interactions that may have contributed to changes in their population structures and changes in rates of predation on them observed since the late 1970's.

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Table 1. Characteristics of summer and autumn sampling stations where YOY Pacific herring and walleye pollock were collected in 1994 and 1995 from Prince William Sound, Alaska.

Abbreviations: T = Trawl, D = Dipnet, B = beach seine, NE = Northeast, C = Central, SW = Southwest. Ten fish per species were examined from each station. Zooplankton were collected at most fishing stations only in 1995; numbers in parentheses indicate adjacent stations substituted when zooplankton were not collected.

Table 2. Size and feeding attributes for allopatric and sympatric YOY walleye pollock and Pacific herring (n = 10 each) from PWS stations in summer, 1995 and autumns, 1994-1995. Standard error of the means (SE) in parentheses. Abbreviations as in Table 1.

Table 3. Seasonal fish size and feeding attributes (mean and SE) of YOY walleye pollock and Pacific herring from Prince William Sound in 1994-1995. Measures for autumn allopatric (Allo.) and sympatric (Symp.) subgroups are shown for each species.

Table 4. Horn's Overlap Index values for total numbers and biomass of prey consumed by YOY walleye pollock and Pacific herring caught separately in summer and together in early and late autumn in Prince William Sound, 1994-1995. No summer sympatric fish were available and autumn allopatric fish were not caught in the same year. Overlap greater than 0.60 indicates similar diets (see text).

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Figure 1. Sampling regions and stations for YOY walleye pollock and Pacific herring diet samples collected in Prince William Sound, Alaska. Circles: July-August, 1995; squares: October, 1995; triangles: November, 1994.

Figure 2. Size of YOY walleye pollock and Pacific herring collected seasonally in PWS from sympatric (S) and allopatric (A) aggregations.

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Introduction - Chapter 2

“Forage fishes are abundant, schooling fishes preyed upon by many species of seabirds, marine mammals, and other fish species. They provide important ecosystem functions by transferring energy from primary or secondary producers to higher trophic levels,” (Springer and Speckman, 1997). Walleye Pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasii*) are two members of forage fish communities inhabiting the northeastern Pacific Ocean rim. The roles of these and other species have been studied in the course of damage assessment and ecosystem investigations in Prince William Sound in the years since the March, 1989 *Exxon Valdez* oil spill (Brown et. al, 1996). Although a number of planktivorous species inhabit PWS, pollock and herring are conspicuous for several reasons. Both species support important commercial fisheries as recruited adults in various areas of the Gulf of Alaska, both are important components of marine bird and mammal diets, and historical data show dramatic changes in both their populations (Springer, 1992; Anderson et. al, 1997; Bechtol, 1997). Young-of-the-year (YOY) walleye pollock and YOY Pacific herring are found at the same depths and locations during at least part of the year (Brodeur and Wilson, 1996; Willette et al., 1997; Stokesbury et al., 1998) and both consume zooplankton as their primary prey (Boldt, 1997; Willette et al., 1997; Foy and Norcross, 1998). Because of these similarities and because the frequency and nature of species interactions may be affected as fish populations shift, an investigation of the potential for competition between these two species is important.

The species composition of forage fish populations in the Gulf of Alaska and Prince William Sound (PWS) has undergone a dramatic shift in recent decades. Prior to the late 1970's, the forage fish community was dominated by capelin, *Mallotus villosus* (Anderson et al., 1994; Bechtol, 1997). Environmental variations such as an ENSO event in 1976, followed by increased water temperatures (Niebauer, 1983; Royer, 1993; Bailey et. al, 1995; Piatt and Anderson, 1996), induced changes in the forage fish biota of PWS. Included among these changes were increases in the number of walleye pollock and other demersal fish, a 75% decline in the spawning population of Pacific herring by 1993 (Brown et. al, 1996), and a 50% decrease in overall fish biomass (Piatt and Anderson, 1996). Such dramatic shifts in the composition and abundance of forage fish populations may have cascading effects in marine food webs (Springer and Speckman, 1997; Livingston, 1993).

Decreases in the marine bird and mammal populations of PWS may be related to these changes in fish population structure (Piatt and Anderson, 1996; Oakley and Kuletz, 1996; Iverson et. al, 1997). Apparently, fewer high quality forage fish have been available, and the species composition has changed to one in which the predominant genera (Gadidae) are less energetically valuable prey for marine birds and mammals (Piatt and Anderson, 1996; Anthony and Roby, 1997). This decrease in prey quality may force predators to expend more energy in capturing sufficient resources for successful breeding (Roby et. al 1998).

The ecosystem of Prince William Sound has been the focus of intense research since the *Exxon Valdez* (EVOS) oil spill Natural Resource Damage Assessment (NRDA) studies. This

report stems from the Alaska Predator Ecosystem Experiment (APEX), a multi-disciplinary study which attempted to link current knowledge about the forage fish of PWS with their seabird predators. We describe the feeding of allopatric (single species) and sympatric (multi-species) aggregations of YOY walleye pollock and YOY Pacific herring collected in summer and autumn by trawl in PWS and speculate on their potential for feeding competition. Evidence for competition between YOY fish may support the hypothesis that pollock are supplanting herring as the primary forage fish resource available in PWS.

Materials and Methods - Chapter 2

Field Methods

Fish stomach and zooplankton samples were collected during APEX forage fish population surveys in central, northeastern and southwestern PWS (Figure 1; Haldorson, 1995; Haldorson et. al., 1996). In a pilot study in 1994, we sampled November 7-13 (late autumn) aboard the Alaska Department of Fish and Game R/V *Medeia*; in 1995, we sampled July 20-August 12 (summer) aboard the charter F/V *Caravelle* and October 5-14 (early autumn) aboard the R/V *Medeia*. Hydroacoustic surveys were conducted offshore along a grid of parallel transects spaced at two-mile intervals and ending as near shore as possible. The grid was surveyed twice in summer and once, partially, in the each autumn. Acoustic gear consisted of a 420 kHz Biosonics Model 120-121 echo-integration system, with transducers towed alongside the vessel. Where fish were detected, the vessel either interrupted the survey or returned after the transect was completed to fish with a research scale, mid-water beam trawl. The net was generally fished 20-35 minutes each time. The trawl's effective mouth opening was 50 m², with net mesh sizes diminishing from 5 cm (2") in the wings to 1 cm (3/8") in the cod end. Additionally, a 0.3 cm (1/8") mesh liner was sewn into the cod end, which terminated in a plankton bucket having 500 µm nytex mesh. In summer, beach seine and dipnet samples occasionally supplemented the trawl catches.

Subsamples of forage species from hauls that caught fish were retained for diet studies. Specimens (n = 10 to 15) were preserved in a 10% buffered formalin-seawater solution on board the vessels for later stomach analysis in the laboratory. In 1995, the zooplankton prey spectrum was assessed from dual vertical hauls at each station, using conical nets 0.5 m in diameter with 303 µm mesh in summer and 243 µm mesh in autumn. We towed the nets from a standard of 20 m depth or to the depth at which fish were caught. Zooplankton samples were usually collected within two hours of fish catches. Two ancillary investigations of zooplankton were conducted to examine differences in fish prey resources. In the first, we conducted mesh trials using 105µm , 243µm , and 303µm mesh nets at three stations in summer to test for a mesh size-related difference in density of summer zooplankton. This was done because related studies had employed each of these nets (Willette et. al, 1997; SEA; Sturdevant et. al, 1996) and because we anticipated changing to a smaller standard mesh size in autumn. Secondly, we collected samples to compare zooplankton densities at shallow (< 25 m) and deeper (25 < m < 100) depths at seven stations in summer (95-1-53 to 95-1-62 and 95-1-112) and one station in early autumn (95-2-7;

Table 1). Hydrographic profile data were collected with a Seabird SEACAT CTD to depths down to 200 m (Haldorson, 1995; Haldorson et. al, 1996).

Laboratory Methods

After a minimum of 6 weeks in formalin solution, fish samples were transferred to 50% isopropanol for at least 10 days before stomach analysis was performed. Ten specimens of each species and size class were measured (mm standard fork length, FL; mg wet weight) and the stomachs examined. Size was used to develop age-class categories for the walleye pollock and Pacific herring diet samples; age estimates were corroborated with length frequency plots of all catch data (Haldorson et. al 1997; Smith, 1981). Walleye pollock 20 to 120 mm FL and Pacific herring 60 to 120 mm FL were classified as YOY or age-class 0. Stomachs were excised, weighed and the contents removed. The weight of prey contents was recorded as the difference between full and empty stomach weights. Fish were considered to be feeding if their stomachs contained more than a trace of food. Relative stomach fullness was recorded as integers (1-7) representing 25% increments on a scale from empty to distended. State of digestion was recorded as 1 = partially-digested contents, 2 = mostly-digested contents, and 3 = empty stomachs. Stomach contents and zooplankton samples were identified with a binocular microscope to the highest taxonomic resolution possible and enumerated. We subsampled all zooplankton samples, and stomach samples when practical, using a Folsom splitter to achieve a minimum count of approximately 200 of the predominant taxon. Numbers were expanded and total prey weights were determined by multiplying the number observed by the mean weight per individual taxon (data on file, Auke Bay Laboratory and University of Alaska Fairbanks, Institute of Marine Science).

Analytical Methods

Forage fish were considered to occur in allopatric aggregations if only one species and age-class was caught in a net haul. They were considered to be sympatric if at least two species or two age-classes of the same species (≥ 10 fish each) were caught in the trawl. For this study, we restricted analyses to YOY pollock and herring that were allopatric or that co-occurred only with each other to limit the complexity of trophic interactions. We examined the size of forage fish and their feeding attributes. Size included FL and wet weight. Feeding attributes included five measures of the quantity of food consumed (mean total number and total weight of prey, mean stomach fullness index (rounded to nearest 25%), and prey percent body weight (%BW) expressed as ratios of wet stomach content weight or total prey weight to fish body weight), two measures of feeding frequency (the proportions of feeding fish to non-feeding fish and the proportions of partially- to mostly-digested stomach contents), and prey composition by percent number and percent biomass of prey categories. Zooplankton density per cubic meter (D) was calculated for species, principal prey taxa, and total organisms in each vertical tow using the expanded organism count, X, divided by the volume, V, of a cylinder having 0.5 m diameter and height, h, equal to the depth of the tow:

$$D = \frac{X}{V} = \frac{X}{\pi \times r^2 \times h}$$

Analysis of variance (ANOVA) was the principal tool used to examine for both intraspecific and interspecific differences in YOY pollock and YOY herring size and feeding attributes and in zooplankton density. We compared data between seasons, between allopatric and sympatric aggregation categories, and between sympatric species. For fish size, we tested FL and wet weight. For fish diets, we tested all five measures of food quantity. Chi-square tests were used to test the feeding frequency measures for association between species, seasons or time of day. For time of day tests, we classified samples collected between 08:00 and 20:00 as “day” and those between 20:01 and 07:59 as “night.” Prey composition and selection were assessed graphically. For zooplankton, we also used ANOVA to test for differences in densities and proportional densities of principal taxa between seasons (summer and early autumn, 1995), between mesh sizes, and between depths sampled. Data were transformed ($\ln x+1$, rank or square root) in order to meet the assumptions of ANOVA. Post hoc Student-Newman-Keuls (SNK) comparisons were performed when significant differences were indicated ($p < 0.05$) in order to determine where they occurred. We present the means of raw data, even when tests were performed on transformed data.

Feeding selectivity of allopatric and sympatric aggregations of pollock and herring was calculated for summer and early autumn, 1995, when zooplankton were collected concurrently at the fish sampling stations. Occasionally, in summer, zooplankton samples from adjacent stations were substituted for those fishing stations without explicit prey samples (Table 1). We used Strauss’ Linear Selection Index, L_o (Strauss, 1979), a measure varying from -1 to +1. Negative values indicate no preference and positive values indicate preference:

$$L_o = r_i - p_i,$$

where r_i = percentage of prey resource I in the diet, and p_i = percentage of prey resource I in the environment. Prey resources for selection were defined as the species, stages and sizes of prey pooled into principal taxa.

Feeding overlap between species and within species between fish in allopatric and sympatric aggregations was described using Horn’s Overlap Index (Horn, 1966; Krebs, 1989; Smith and Zaret, 1982). This index minimizes bias due to changing numbers of resource categories and resource evenness. Overlap was computed at two levels, with prey resources defined at the lowest level (species, stage and size) and at a pooled level (principal taxa). Horn’s Overlap Index values, R_o , are expressed from 0 (no overlap) to 1 (total overlap) for predator species j and k :

$$R_o = \frac{\sum (p_{ij} + p_{ik}) \times \ln(p_{ij} + p_{ik}) - \sum p_{ij} \times \ln p_{ij} - \sum p_{ik} \times \ln p_{ik}}{2 \times \ln 2}$$

where p_{ij} = proportion resource I is of the total resources utilized by species j , and p_{ik} = proportion resource I is of the total resources utilized by species k . We considered R_o values > 0.60 to indicate similar use of resources and $R_o > 0.75$ to indicate very similar use of resources.

Results - Chapter 2

Seasonal differences in the aggregations of YOY walleye pollock and Pacific herring sampled from PWS were apparent. Fish were not collected from both allopatric and sympatric aggregations in all seasons (Table 1). In summer, 1995, when 62 total trawl hauls were made, no sympatric YOY pollock and YOY herring were caught in the 18 hauls catching sufficient samples of either one. Allopatric YOY pollock were collected at 12 summer stations ($n = 120$ diet samples) in the central region and allopatric YOY herring were collected at one central and one northeastern station ($n = 20$ diet samples; Figure 1). In four additional summer hauls, YOY pollock or herring were caught with other age classes or species (Pacific sandlance, capelin, Pacific tomcod). However, in early autumn (October, 1995, 11 trawl hauls) and late autumn (November, 1994, 14 trawl hauls), these species were caught both allopatrically and sympatrically. Sympatric YOY pollock and herring were caught in 36% of 11 autumn hauls catching YOY of these species, at two stations in the northeastern region of PWS in both early and late autumn ($n = 20$ diet samples per species and season). Allopatric fish were collected in different autumn months, the allopatric pollock ($n = 10$) in late autumn (southwestern region) and the allopatric herring ($n = 10$) in early autumn (central region). Additional hauls caught YOY pollock and herring that we excluded from this study because of our restricted definitions of allopatric and sympatric and our objective to examine only YOY pollock-herring trophic interactions. In early autumn, four additional hauls caught YOY pollock and herring, three as co-occurring species, but other age classes and either capelin or eulachon were also caught; in late autumn, one haul caught co-occurring YOY pollock and herring with eulachon.

In addition to species composition, other qualities of the catches varied, including numbers caught, relative species composition, sampling time and sampling depth. In summer, the number of pollock caught in trawls varied by two orders of magnitude between stations, from 22-1689 per haul. Herring catches could not be compared to trawl catches because they were collected by dipnet or beach seine. In autumn, between 14 and 4156 of each species was caught at a station, but YOY pollock and herring numbers were not consistently partitioned among sympatric catches. Similar numbers of each species were caught at some stations, while, at others, an order of magnitude greater number of one species was caught (Table 1). Samples were collected during different periods of the day and at different depths in summer and in autumn. In summer, most samples were collected by early evening. Summer pollock were mostly caught offshore at 50-80 m trawl depths ($\bar{6} = 60$ m), while herring were caught in alternative gear at the surface and

nearshore (Table 1). In autumn, most samples were collected shortly before midnight, at a mean depth of 30 m, in bays. The autumn allopatric samples were collected earlier in the day and deeper than the autumn sympatric samples.

Seasonal Comparisons

YOY pollock were generally larger than YOY herring during a season (Figure 2), but intraspecific patterns of size across seasons differed (2-way ANOVA interaction, $p < 0.05$). Although both species FLs and weights were significantly greater in early or late autumn than in summer (1-way ANOVA, SNK multiple comparisons, $p < 0.05$), only pollock size differed between early and late autumn. Mean FLs of both species were approximately 60% longer in autumn than in summer (Tables 2 and 3; Figure 2). In late autumn compared to early autumn, pollock FL was approximately 14 mm greater, while wet weight was approximately 50% greater ($p < 0.05$). For herring, neither lengths nor weights differed between early autumn and late autumn ($p > 0.05$).

Seasonal patterns in feeding attributes differed consistently for the two species. The stomachs of the majority of YOY pollock and herring examined did contain food, but full stomachs (mean fullness of 100%) were not common for either species (Table 2). For pollock, the proportion of non-feeding individuals was not associated with season (χ^2 test, $p = 0.2296$), but for herring, it was associated with season (χ^2 test, $p = 0.0004$). Herring in late autumn were the only group with a higher proportion of non-feeding fish than feeding fish (Table 3). Pollock and herring had very similar proportions of feeders in summer and early autumn (80%), but in late autumn, the proportion of non-feeding herring was more than twice the proportion of non-feeding pollock.

Interspecific differences in seasonal feeding were also evident from tests on stomach fullness index, both %BW ratios, and total numbers and weights of prey (2-way ANOVA interactions, $p \neq 0.0276$). Among pollock, only two significant differences were found across seasons, both between summer and late autumn. Prey %BW and content %BW were both above 1% in summer and below 1% in the autumn months, but only the late autumn values were significantly lower than the summer values (SNK multiple comparisons, $p < 0.05$; Table 3). No differences between summer and early autumn or between early and late autumn feeding attributes were significant for pollock. Pollock stomachs were approximately half full in each season and the total number and biomass of prey consumed did not differ (Figure 3). Pollock prey numbers were highly variable and prey weights were similar in each month. Mean prey number ranged from a high of approximately 294 in summer to a low of 63 in early autumn, while mean prey weight ranged from approximately 34 to 39 mg.

Among herring, trends toward lowest feeding in late autumn were significant, but trends toward lower feeding in early autumn compared to summer were not significant. All five food quantity measures were significantly lower in late autumn compared to summer and in late autumn compared to early autumn, but did not differ between summer and early autumn (SNK multiple comparisons, $p < 0.05$). Herring stomachs were fullest in summer (75%), were half full in early

autumn, but contained only trace amounts of food in late autumn. Herring %BW measures were also greatest in summer (\$ 1.9%) and least in late autumn (# 0.3%). Similarly, mean total numbers and weights of prey decreased seasonally for herring, from 3011 prey weighing 271.1 mg in summer, to 528 items weighing 82.2 mg in early autumn and 23 items weighing 13.2 mg in late autumn (Figure 3; Table 3).

Individual fish digestion data were pooled across seasons to test for differences in diel feeding patterns. The condition of stomach contents differed significantly between the species by time of day. Pollock had greater proportions of mostly-digested contents during the day compared to the night (χ^2 test, 2 d.f., $p = 0.0033$). Conversely, herring had marginally greater proportions of mostly-digested contents during the night compared to the day (χ^2 test, 2 d.f., $p = 0.0670$). However, the proportions of feeding and non-feeding fish were not different by day and night for either species (χ^2 test, 2 d.f., $p = 0.7877$).

Allopatric/Sympatric Comparisons

Patterns in size and feeding of fish in autumn allopatric and sympatric aggregations varied with species. We did not pool sympatric fish from early and late autumn for comparison to allopatric groups because of the intraspecific differences in size and feeding measures between these seasons. For late autumn pollock, FLs of allopatric and sympatric fish were not different (t-test, $p > 0.05$), but fish were approximately 1.5 g lighter ($p = 0.0494$) in sympatric aggregations compared to fish in allopatric aggregations. For early autumn herring, no differences were observed between the sizes of allopatric and sympatric fish ($p > 0.05$; Figure 2; Table 3).

We also found differences in feeding between the allopatric and sympatric pollock from late autumn but not between the allopatric and sympatric herring from early autumn. Among pollock, the late autumn allopatric fish consumed the greatest numbers and biomass of prey of all autumn pollock (Figure 3; Table 3). All other feeding measures were also consistently greatest among the allopatric pollock. Feeding measures for late autumn sympatric pollock were significantly lower than values for both the late autumn allopatric and the early autumn sympatric pollock (1-way ANOVA, $p < 0.0002$). With one exception, the late autumn allopatric values were not significantly different from the early autumn sympatric values ($p > 0.05$). Prey numbers were the only measure of these allopatric pollock that differed significantly (greater, $p < 0.05$) from prey numbers of early autumn sympatric pollock (Figures 4 and 5). The late autumn allopatric pollock consumed more than 700 prey items (71 mg), while late autumn sympatric pollock consumed 13 prey items (16 mg) and early autumn sympatric pollock consumed 63 prey items (39 mg). The late autumn allopatric pollock and the early autumn sympatric pollock had stomachs that were more full (\$75%) and mean %BW values that were higher (\$ 0.8%BW) than these measures for late autumn sympatric fish (25% full, # 0.4% BW; Table 3).

The allopatric-sympatric feeding pattern was different for herring than for pollock. The early autumn allopatric herring consumed the greatest prey biomass, but not prey numbers, among all the autumn herring (Figure 3; Table 3). The allopatric and sympatric values from early

autumn were not significantly different from each other, but both of these values were greater than the late autumn sympatric values ($p < 0.0001$). Content %BW was the only significantly different measure between allopatric and sympatric herring in early autumn. In early autumn, herring stomachs were $\approx 50\%$ full whether allopatric or sympatric, while in late autumn, sympatric herring stomachs were less than 25% full. Allopatric herring consumed 386 prey items (103 mg), while sympatric herring consumed 599 prey items (≈ 72 mg), in early autumn. In late autumn, sympatric herring consumed ≈ 23 prey items (13 mg). Herring mean %BW (either value) was also lower for late autumn sympatric fish ($= 0.3\%$ BW) than for the other groups ($\approx 0.9\%$ BW).

In tests restricted to sympatric fish, we again found strong seasonal differences, but few interspecific differences in feeding between the pollock and herring; no season-species interaction term was significant for sympatric fish (2-way ANOVA, $p > 0.05$). All five measures of food quantity were significantly greater among early autumn sympatric fish than among late autumn sympatric fish ($p < 0.0001$), but only the fullness index differed between species. Pollock stomachs were slightly ($< 25\%$), but significantly more full in sympatric aggregations than herring stomachs ($p = 0.0377$). The proportion of non-feeding sympatric individuals was not associated with species (χ^2 test, $p = 0.2039$), and no interspecific differences were found for prey numbers or biomass, or prey %BW (ANOVA, $p > 0.05$).

Young-of-the-year pollock and herring prey compositions were similar in both summer and autumn (Figures 4 and 5), but prey composition differed between seasons. Small prey predominated in summer and larger prey in autumn, especially in terms of biomass composition. In summer, small calanoid copepods (*Pseudocalanus* spp., *Centropages abdominalis*, *Acartia longiremis*) dominated the diets both numerically and in terms of prey biomass. Among pollock, small calanoids comprised 55% by number and 57% by weight. By number, most of the remainder of summer pollock diet was comprised of invertebrate eggs (39%); by weight, the remainder was large calanoids (principally *Calanus pacificus*, *C. marshallae* and *Metridia pacifica*), fish, hyperiid amphipods and euphausiids (both larvae and older stages, including *Thysanoessa* sp.). Small amounts of other prey, including larvaceans, gastropods, and chaetognaths, were also commonly consumed by pollock. Among summer herring, small calanoids comprised proportionally more of the diet than among pollock. Overall, small calanoids made up 77% by number and 88% by weight of herring diet; they were the sole taxon consumed by the YOY herring at Eleanor Island station 110 (Table 2). Other small prey (cladocerans, bivalve larvae, and invertebrate eggs) formed most of the rest of the herring diet, with minor contributions of decapod larvae, gastropods, hyperiids, and euphausiid larvae consumed. We could not compare allopatric and sympatric diets in summer because of lack of samples.

In early autumn (1995) and late autumn (1994), pollock and herring fed from the same prey categories. Larvaceans and large calanoid copepods numerically dominated the autumn diets of both species, comprising 57-91% of prey. Euphausiids and large calanoids dominated the autumn diets in terms of biomass proportions (Figs. 4 and 5). Compared to these prey taxa, small calanoids comprised smaller proportions of the diet (up to 37% of prey number and 9% of prey

biomass), and hyperiids occasionally contributed up to 11% biomass. Euphausiids included *Thysanoessa raschii*, *T. spinifera* and unidentified juveniles and adults, but no larvae. Large calanoids included the same species present in summer diets, as well as *M. ohkotensis* and *Neocalanus* spp., while small calanoids included *Pseudocalanus* spp., *Acartia longiremis*, and *Oithona similis*. Invertebrate eggs (the majority of “other”) were present less frequently in autumn diets than in summer diets. Some differences in diet composition between early and late autumn did exist, however. Early autumn diets included proportionally more biomass from large calanoids, while late autumn diets included proportionally more biomass from euphausiids; larvacean numbers tended to be less prominent in early autumn than in late autumn.

Substantial interspecific and intraspecific diet overlap was observed for YOY pollock and herring in both early autumn (1995) and late autumn (1994). Higher values of Horn’s Overlap Index were indicated when prey species were grouped into principal taxa (Table 4). In summer, Horn’s Overlap Index indicated very similar diets ($R_o > 0.76$) between allopatric species in terms of numbers and weights of prey species or principal prey taxa. In early autumn, no numeric overlap between sympatric pollock and herring was observed ($R_o < 0.60$). In late autumn, diets of sympatric species were similar ($R_o > 0.69$) at both stations where they co-occurred based on numbers of prey consumed from principal taxa. Mean numeric overlap for the late autumn sympatric species was approximately twice that of the early autumn sympatric species ($R_o = 0.97$ versus 0.43). Based on biomass of the prey items consumed from principal taxa, significant diet overlap was observed between sympatric species at both early autumn stations and one late autumn station. Overall, diets of sympatric pollock and herring overlapped less in terms of biomass in early autumn ($R_o = 0.69$) than in late autumn ($R_o = 0.95$). Diet overlap between allopatric and sympatric pollock or herring collected in the same season was extensive at the principal taxon level for herring in early autumn in terms of biomass ($R_o = 0.93$) and for pollock in late autumn in terms of prey number ($R_o = 0.91$).

Zooplankton Composition

The densities per cubic meter and the composition of zooplankton present in the water column were compared between summer (303 μ m mesh) and early autumn (243 μ m mesh), but no data were available for late autumn. Total zooplankton density (ln-transformed) was not different (1-way ANOVA, $p = 0.1685$) between summer ($n = 37$) and autumn ($n = 8$). Mean total densities were 1184 ± 138 organisms \cdot m $^{-3}$ in summer and 1414 ± 185 in early autumn (Figure 6). Taxa were less diverse in summer than in autumn, but small calanoids predominated in both seasons. Small calanoids were a significantly ($p < 0.0001$) greater proportion of the total in summer than in early autumn (84% vs. 58%), although their absolute density did not differ between seasons (1018 ± 133 vs. 828 ± 130 organisms \cdot m $^{-3}$; $p < 0.05$). Gastropods (*Limacina helicina*) were second most abundant in summer, but followed large calanoids and bryozoan cyphonautes larvae in abundance in autumn. No other taxon contributed more than 5% in summer. Gastropods numbered 60 ± 10 m $^{-3}$ (5.8% total) in summer and 96 ± 19 m $^{-3}$ (6.8%) in early autumn; neither density nor proportional density of gastropods differed between seasons ($p > 0.05$). Large calanoids were an order of magnitude less abundant in summer than in early

autumn ($p < 0.0001$), when they formed 13% of total zooplankton (204 ± 60). Larvacean density and percent density were each approximately three times lower in summer (14 ± 4 organisms*m⁻³) compared to early autumn (45 ± 11 organisms*m⁻³; $p < 0.0194$). Cladocera were present only in summer (approximately 5% total) and cyphonautes were present only in early autumn (~16% total, 205 ± 50 organisms*m⁻³). Hyperiid amphipods, euphausiid larvae, chaetognaths, and barnacle and decapod larvae were sometimes present in low numbers (< 2 organisms*m⁻³).

Mesh size-related differences in zooplankton density were observed in summer. Total density estimates decreased significantly (1-way ANOVA, $n = 11$, $p = 0.0008$), by an order of magnitude, from the smaller mesh nets to the larger mesh nets; all pairs of estimates were different (SNK, $p < 0.05$). Mean total densities decreased from approximately 41,000 organisms*m⁻³ estimated from 105 μ m mesh to 11,000 organisms*m⁻³ estimated from 243 μ m mesh to 2,300 organisms*m⁻³ estimated from 303 μ m mesh. Small calanoids were always the most abundant organisms. Among all taxa, net size-selectivity was observed only for small calanoids and for “other”; declines in density estimates with increasing mesh size were highly significant ($p = 0.0001$) for small calanoids and marginally significant ($p = 0.0711$) for “other”. Small calanoid density estimates decreased 4x between successive mesh sizes. However, relative zooplankton composition was the same for all mesh sizes, with small calanoids contributing 79-90% of total organisms ($p = 0.2886$). For all other principal zooplankton taxa (large calanoids, larvaceans, cladocerans, and gastropods), neither the percentage contribution nor absolute density differed between the three mesh sizes (1-way ANOVA, $p > 0.05$).

The depth of the water column sampled also impacted the zooplankton density estimates in each season. At the seven summer stations and one autumn station where a shallow (20-25m) pair of zooplankton tows was followed by another pair of tows to the depth where fish were sampled (50-100 m), mean total densities were always greater in the shallower water column, and lesser in the deeper water column. In summer, the total density per cubic meter estimated from shallow hauls was more than twice the estimate from deep hauls (1371 ± 191 vs. 645 ± 91 organisms*m⁻³; 2-way ANOVA, $p < 0.0001$). In early autumn, total densities at shallow depths (25 m) were marginally greater (t-test, $n = 4$, $p = 0.1098$) than at deeper depths (1299 ± 64 vs. 1064 ± 56 organisms*m⁻³). Differences in the abundance, but not the percentage composition, of principal taxa with depth were also observed. In summer, small calanoid abundance was twice as high nearer the surface (1175 ± 181 vs. 550 ± 87 organisms*m⁻³; $p = 0.0002$); small calanoids comprised approximately 84% of total zooplankters at each depth (ANOVA, $p = 0.7365$), however. In early autumn, both the absolute density and the proportion of small calanoids were at least marginally greater nearer the surface ($p < 0.0530$); small calanoid densities were 685 ± 48 (53%) and 426 ± 40 (40%) organisms*m⁻³ in shallow and deep water, respectively. Large calanoids exhibited the reverse pattern in early autumn, but not in summer. In summer, the abundance and proportion of large calanoids did not differ ($p > 0.05$) between depths, density being 36.9 ± 6.7 (3.3%) in shallow water and 27.6 ± 56 (4.7%) organisms*m⁻³ in deep water. In early autumn, the abundance of large calanoids was significantly ($p = 0.0036$) greater in deep water than in shallow water (176 ± 3 vs. 104 ± 3 organisms*m⁻³); the proportional density of large calanoids was also significantly ($p = 0.0099$) greater in deeper water in autumn (16.6% vs.

8.1% of the total). Gastropods were the only other taxon that comprised more than 10% of the total zooplankton in either season. Gastropod numbers were greater ($p < 0.0136$) in both seasons nearer the surface, but proportions did not differ with depth ($p > 0.05$). Gastropod densities in shallow and deep water were 99.4 ± 22.8 vs. 36 ± 5.3 organisms $\cdot\text{m}^{-3}$, respectively, in summer, compared to 141.4 ± 4 vs. 84 ± 5.3 organisms $\cdot\text{m}^{-3}$ in autumn. Larvaceans showed no biologically meaningful, significant differences between depths for either absolute or proportional density in either season ($p > 0.05$). Cladoceran density was marginally greater ($p = 0.0329$) near the surface compared to deeper water in summer (24.9 ± 8.9 vs. 6.0 ± 1.3 organisms $\cdot\text{m}^{-3}$, but proportional density was not different ($p > 0.05$); cladocerans were absent in autumn. Cyphonautes larvae were present only in autumn and showed no differential abundance by depth (approximately 300 organisms $\cdot\text{m}^{-3}$; $p > 0.05$).

We also compared densities of important prey taxa among stations within seasons as a measure of prey patchiness. Summer stations spanned the central sound from Applegate Rocks to Storey Island; autumn stations were in the northeastern region. Total zooplankton density differed significantly (2-way ANOVA, $p = 0.0088$) among summer stations, but no interaction existed between station and depth ($p = 0.2448$). Zooplankton densities at East Eleanor Island (station 62) were higher ($p > 0.05$) than at all stations except Montague Point (station 53). Density of small calanoids at station 62 was significantly higher ($> 2x$) than at all others except station 53 (2-way ANOVA, $p = 0.0049$). Inter-station differences in density of large calanoids and gastropods also existed ($p < 0.0005$), but the patterns were more complex. For large calanoids, an interaction between station and depth was found ($p = 0.0057$). At stations 54 and 62, density of large calanoids was higher at deep locations than at shallow depths, the reverse of the pattern at the remaining summer stations. Large calanoid density at station 56 was higher than at all other summer stations, while it was lower at station 62 than at all stations except station 58. For gastropods, densities at stations 54 and 57 were lower than at three stations (56, 58, and 62). Larvacean density did not differ significantly ($p = 0.1712$) between stations. No other consistent pattern of differences between summer stations was observed. Among early autumn stations, sampling depths ranged from 25 m to 80 m. Total density at one sympatric station, Galena Bay, was significantly (ANOVA, $p < 0.05$) greater ($\sim 2x$) than at either of the other two stations. This pattern was repeated for large calanoids ($\sim 4x$) and small calanoids ($\sim 2x$; $p < 0.0149$), but no difference existed for larvaceans ($p = 0.4462$).

Selection by pollock and herring from among the zooplankton taxa present in 20 m zooplankton tows was noted in both summer and early autumn, 1995 (Figure 5). Summer pollock avoided small calanoids and moderately selected for large calanoids, gastropods and larvaceans. Nonetheless, pollock diet was made up of $> 50\%$ small calanoids. Summer herring were not strongly selective of any prey category. Their predominant prey, small calanoids, was consumed in close proportion to its availability. In early autumn, pollock strongly selected for large calanoid copepods and herring strongly selected for larvaceans, the largest components of their diets. Small calanoids were avoided by both species. Allopatric herring were more selective of large calanoids than were sympatric herring in early autumn, while selection for larvaceans was similar for both groups. A strong trend towards selectivity or avoidance was not observed for any

other prey category, but pollock consumed hyperiids more frequently than euphausiids in summer and both pollock and herring consumed euphausiids more frequently than hyperiids in autumn.

Discussion - Chapter 2

In the summer of 1995, diets of YOY walleye pollock and Pacific herring in allopatric aggregations were very similar. Prey of both species were predominantly composed of small calanoids, with smaller proportions of a variety of organisms. These results are supported by other work from PWS in 1994-1996 and by additional, widespread, studies. Calanoids were the dominant prey of both YOY pollock and herring by percent numbers, weight and frequency of occurrence in late summer, 1994, in PWS, and were the basis for high diet overlap between the species (Willette et. al, 1997). Elsewhere, pollock 30-70 mm in length caught during spring and summer in Japanese waters consumed virtually all types and sizes of calanoid copepods inhabiting the area, as well as larval euphausiids and a variety of other small prey (Kamba, 1977). In late summer, pollock 60-93 mm caught in the Kodiak Island-Alaska Peninsula region of the eastern North Pacific had diets in which small calanoids comprised over 75% of prey numbers, but euphausiids were already more than 75% of prey biomass (Livingston, 1985). Similarly, small calanoids were the principal prey (percent number or volume) of YOY pollock 33-97 mm in length in southeastern Alaska between August-October, with one species, *Acartia clausi*, particularly important (Krieger, 1985).

YOY herring also depend on small calanoid prey. Small calanoids comprised the greatest dietary biomass of fish from four bays in PWS in summer, although spatial differences in the diets were observed (Foy et. al, 1998). In another PWS study, most of the diet of beach seined YOY herring was made up of small calanoids, but larvaceans were selected in greater proportions than they were present in zooplankton samples (Sturdevant et. al, 1999). In the Strait of Georgia in early summer, calanoid copepods predominated (> 80% occurrence) in YOY herring diets; other principal prey included amphipods, invertebrate eggs and euphausiids, plus barnacle larvae later in summer (Haeghele, 1997). Depending on the habitat occupied, early YOY herring diet may include epibenthic prey, such as harpacticoid copepods and gammarid amphipods, as well as pelagic prey, such as calanoid copepods, cladocerans and oikopleurans (Blaxter and Hunter, 1982; Lassuy, 1989). In southern B.C., age-0 herring consumed whatever plankters were readily available (Wales, 1936), with calanoids and barnacle larvae being most important.

Despite the similarity of their summer diets in PWS, we observed some differences in prey selection between the YOY pollock and herring. Some of these probably relate to diel vertical distributions of predator and prey. The summer herring were located at the surface where densities of small calanoids, their main prey, were twice as high as deeper in the water column. Higher concentrations of zooplankton were also observed below the surface off the Oregon Coast (Petersen and Miller, 1970). Both herring and pollock perform diel vertical migrations, but the time of day and depth of feeding of juveniles are not well known (Willette et. al, 1997; Merati and Brodeur, 1996). Herring are primarily visual feeders requiring minimum light levels to feed (Blaxter, 1982). Young herring vertical distribution varies widely in both day and night, and they

respond to prey distributions that may be correlated with thermocline depth (e.g., Fossum and Johannessen, 1979, in Munk et. al, 1989). For example, when prey were distributed throughout the water column, herring larvae migrated up to depths of optimal light intensity for feeding; when their copepod food source was concentrated at 40 m, the fish migrated down to this depth only at noon, when light levels were sufficient for feeding (Munk et. al, 1989). In our study, herring were located in more dense prey patches and where light for feeding was most intense, compared to the deeper pollock. The herring fed non-selectively--small calanoids were present in their diets in similar proportions as they were present in the environment. Smaller individuals' diets were limited to this taxon, while larger individuals' diets were more diverse. Judging by the relatively less-digested condition of herring stomach contents by day compared to night, these surface aggregations occurred at the principal time of feeding.

The summer depth of pollock in our study contrasted with that of herring and may relate to different feeding rhythms and prey preferences. Pollock were located in relatively deep water where all of the taxa they consumed were less abundant than at the surface. Similar to herring, small calanoids made up the largest single dietary component of pollock, but these prey were avoided relative to their availability. Pollock sometimes selected large calanoids, but these prey were not more abundant at depths where the fish were located. Abundance of the other prey selected by pollock was either no different (larvaceans) or was lower (gastropods) at depths where the fish were located. Just as for herring, feeding conditions can affect the vertical distribution of juvenile pollock, along with other factors such as predator presence, light, turbidity, and pressure (Olla et. al, 1996). In the Bering Sea, juvenile pollock were located between the thermocline and neustonic layer, a preference partly regulated by temperature. Vertical movement though a thermocline depended on relative availability of food and was less likely to be performed by the smaller juveniles (Bailey, 1989; Olla and Davis, 1990; Sogard and Olla, 1996; Olla et al, 1996). Avoidance of light increased and avoidance of cold water decreased with growth, especially under conditions of low zooplankton. Pollock prey preferences, zooplankton distribution at the time of sampling, and the mostly-digested condition of their prey suggested that pollock in our study were not feeding principally during the day; instead, they may have fed the night before.

Changes in zooplankton composition from summer to early autumn were reflected in fish diets. Although they were highly abundant in both seasons, small calanoids were not selected, but were eaten randomly or avoided by both fish species. The proportional density of small calanoids in the zooplankton declined by nearly 30% from summer to early autumn, and the proportion consumed by fish was likewise much reduced. In contrast, both large calanoids and larvaceans were more abundant in zooplankton samples in early autumn than in summer and, along with euphausiids, formed larger dietary components at that time. Large calanoid copepods were selected for by both species in autumn, especially by pollock. Larvaceans were selected by pollock in summer and by herring in autumn. These species continue to exhibit similar prey requirements and minimal prey partitioning during seasonal changes in the available prey suite.

The changes in diet that we observed from summer to early autumn may also relate to the

seasonal increase in fish size and energy requirements, as well as to changes in zooplankton prey spectrum. The autumn prey composition of pollock that we observed is very similar to the September diet of YOY pollock in the Gulf of Alaska (Merati and Brodeur, 1996). In that study, increased fish size was correlated with decreased predation on copepods and increased predation on larvaceans and euphausiids, and geographic differences in diet were pronounced. In southeastern Alaska, larvaceans were consumed frequently by pollock only in September, and were never a high percentage of numbers or volume of prey; large calanoids (numbers) and euphausiids (volume) were more substantial in late autumn-winter juvenile pollock diets (Krieger, 1985). By winter, epibenthic prey, including mysids, shrimps, cumaceans and chaetognaths, may also be incorporated in the diet as vertical distributions of the fish change and pelagic prey become scarce (Krieger, 1985; Merati and Brodeur, 1996). For YOY herring, predation on calanoids by younger fish and on euphausiids by older fish is also often reported (Lassuy, 1989; Haegele, 1997; Wailes, 1936). The predominant prey biomass of YOY herring in other PWS studies changed from small calanoids in June to larvaceans in October (Foy et. al, 1998), while euphausiids were minor dietary components (Foy et. al, 1998). Malacostracans (including mysids and euphausiids) formed larger portions of the prey biomass in November (Foy and Paul, 1999). A common pattern of diet transition in early autumn or with larger size was observed in the above studies of herring and pollock as well as ours: small calanoids were supplanted by larger calanoids, larvaceans and larger crustaceans.

Differences in the species' diets could also have been related to specific prey attributes, such as size, life history stage or vertical distribution, and to regional or habitat differences the prey available within PWS. Both the fish and many of their invertebrate prey undergo diel vertical migration (DVM). Other studies have correlated size-related differences in the vertical distribution of herring larvae with shifts to larger prey that had different migration patterns (Fortier and Leggett, 1983 in Munk et. al, 1989). During both summer and autumn in our study, pollock and herring consumed a variety of calanoid species with varied life history patterns and whose sizes assigned them to both small and large size classes (< 2.5 mm and ≥ 2.5 mm total length, TL, respectively). Both large and small calanoids can alter their migration patterns in response to environmental conditions, including predator presence (e.g., Bollens et. al, 1992; Frost and Bollens, 1992). Migration patterns of calanoids can also vary between species or life history stages (e.g., Hattori, 1989; Bollens and Frost, 1991; Neill, 1992) and within species in response to food levels (Dagg, 1985; Dagg et. al, 1997). Among two commonly-consumed large calanoids, *Metridia lucens* was found deeper than *Calanus pacificus* during both day and night; *M. lucens* migrated in a consistent pattern, and was not found at the surface during the day as *C. pacificus* sometimes was. Juvenile herring preferred *Calanus*, but predator-avoidance was not thought to be the factor controlling the distribution of *M. lucens* (Bollens et. al, 1993). Among small calanoids, conversely, the diverse behavioral repertoire of *Pseudocalanus newmani* (Frost and Bollens, 1992) and the strength of DVM of *Acartia hudsonica* (Bollens et. al, 1992) were thought to be avoidance responses to teleost and invertebrate predators, not responses to light or food. These variations in behavior suggest that a complex array of interactions between predator and prey, as well as between potentially-competing predators, can influence fish diets.

Other characteristics besides density and size influence the selection of prey taxa. Larvaceans are a highly visible taxon (Bailey et. al, 1975) that is relatively small when without their mucous houses. Although they are gelatinous, their caloric value per unit weight is closer to that of euphausiids, hyperiids, calanoids, and gastropods (*Limacina helicina*) than to cnidarians or ctenophores (Davis et al., 1998), possibly because they concentrate phytoplankton prey (Knoechel and Steel-Flynn, 1989). Individual larvacean weight is on the order of 10-100x lighter than a large calanoid copepod and 2x lighter than a small calanoid (data on file, Auke Bay Laboratory). Therefore, many more larvaceans must be consumed to accumulate the equivalent calories obtained from the crustaceans. Larvaceans may appear to be selected for if fish have fed in a front or other hydrographic feature that can maintain prey aggregations (Alldredge, 1982). Conversely, fish may avoid the predominant prey available if other, less abundant taxa are more attractive or if the energy expended to consume sufficient calories as small calanoids exceeds that expended to capture less motile prey, such as larvaceans, or larger, highly motile prey, such as large calanoids. Visual feeders may also feed opportunistically on dense organisms in the dark (Batty et. al, 1986). The presence of high numbers of minute prey that escaped our plankton nets (e.g., bivalve larvae and invertebrate eggs < 100 μm in diameter), is an often-noted (Krieger, 1985; Grover, 1990, 1991; Merati and Brodeur 1996; Haegele, 1997) example of opportunistic feeding by filtration rather than by selection (Batty et al., 1986). Foy et. al (1998) hypothesized that herring could achieve greater energy intake by selective feeding during periods of low prey diversity and high prey density, compared to periods of high prey diversity and low prey density, even if stomachs were not as full.

Besides calanoid mesozooplankton, two macrozooplankters which perform diel vertical migrations, euphausiids and hyperiid amphipods, appeared in the diets of pollock and herring in all seasons (Figures 4 and 5). Little is known about these macrozooplankters in PWS, and our qualitative data do not allow us to calculate selection. One would expect to observe different size classes of these taxa in fish diets during much of the year, however, since a variety of euphausiid and amphipod species produce multiple broods annually (Wing, 1976; Tanasichuk, 1998a). They were not a substantial biomass component of the summer diets because the small, early stages were consumed most often; the larger stages contributed more prey biomass in autumn. The early stages of euphausiids and hyperiids were captured in low numbers in plankton nets and older specimens were captured in trawls and NIO nets in both seasons. They were patchily distributed and a regional distribution gradient was exhibited by euphausiid species (Paul, 1995; Dr. T. C. Shirley, personal communication). Adult (15-25 mm TL) *Euphausia pacifica* and four species of *Thysanoessa* were captured in all seasons (Haldorson et. al, 1996). Hyperiids were not identified and were only enumerated from late autumn trawls (Paul, 1996).

Since sampling time of day differed between seasons, diel period may partially account for seasonal differences in the appearance of euphausiids and other prey in the diet. In summer, sampling coincided with an unlikely time for predation to occur: during daylight, when the distributions of vertically migrating predator and prey did not overlap. In summer, euphausiids were captured in only 7 out of 62 trawls (11%). These were collected below the mean depth of our pollock catches, 60 m. Euphausiids were present in both the northeastern and southwestern

regions of the sound, but were not caught in the central region or at any of our fish stations. Summer fish may have been too small to feed on juvenile and adult euphausiids, and/or they may not occupy the same habitat during the day.

Autumn fish were larger than summer fish and the small calanoids that were their former principal prey were not only proportionally less abundant but were probably no longer an appropriate size to sustain them (Parsons and LeBrasseur, 1973). In early autumn, all groups of both species avoided small calanoids, and all groups of herring selected larvaceans. However, feeding and selection patterns differed between aggregations within species. The deeper, allopatric herring collected in daytime were the only ones that strongly selected for large calanoids, although these prey were less abundant at the allopatric station than at the sympatric stations. The proportion of large calanoids in the allopatric and sympatric herring diets was not different, however.

We found little indication that one species fed poorly compared to the other when they co-occurred. We observed the same frequency of feeders for pollock as for herring in sympatric aggregations and diets overlapped extensively. The two species' diets were also similar when they occurred allopatrically, in either summer or autumn. Diet composition changed little in the presence of a potential competitor, but a few differences between early autumn diets of the two sympatric species existed. In contrast to herring, the sympatric pollock did select large calanoids, especially at Galena Bay, where this prey taxon was most abundant and where catches of YOY pollock were the highest. We also observed that *Metridia* spp. were selected more strongly by pollock than by herring, possibly indicating a difference in feeding time or habitat utilization between the species. Sympatric pollock also consumed proportionally more euphausiid biomass than the sympatric herring. Large calanoids and euphausiids could have been consumed at different feedings, particularly if their vertical distributions overlapped with the fish vertical distributions at different times. Changes in prey composition with time of day have been noted previously for YOY pollock (Merati and Brodeur, 1996). No differences were apparent in the species or size of euphausiids consumed by different aggregations of fish. These observations suggest that, for the sympatric juvenile herring, interspecific interactions may limit predation on large calanoids, but predation on euphausiids may be limited by fish size.

Euphausiids were a principal prey in terms of biomass, particularly for autumn pollock. Some of the fish in all autumn aggregations consumed euphausiids, the largest and most energy-dense taxon, especially when large calanoid consumption declined in November. Euphausiids may also have been more available in autumn compared to summer. They were caught in trawls much more often in autumn, at four of seven trawl stations in early autumn (57%), and at five of 14 stations in late autumn (36%). They were not caught in the southwestern region in early autumn, but were present in all three regions in late autumn. Among the early autumn stations for which we have fish diet data, euphausiids were not collected at East Naked Island, but the allopatric herring there consumed juvenile euphausiids and amphipods more frequently than three out of the four sets of sympatric fish from Galena Bay and Landlocked Bay, where euphausiids were collected. Overall, despite these prey "advantages," the allopatric herring had very similar prey

composition, did not consume greater quantity of food, and the fish were not larger compared to sympatric herring.

In late autumn, allopatric pollock caught in daytime in deep water had much higher feeding measures than sympatric pollock caught at night in shallow water. Among late autumn stations, amphipods, but not euphausiids, were collected at Icy Bay, yet the allopatric pollock there ate euphausiids and amphipods more frequently than any of the sympatric groups at Galena Bay and Port Gravina, where both amphipods and euphausiids were collected. They ate euphausiids and large calanoids more frequently than sympatric fish, but overall, proportionally less of their prey biomass was euphausiids. Euphausiids made up less than 30% of prey biomass in these allopatric pollock, while in the sympatric pollock and herring, euphausiids comprised approximately 80% of the prey biomass. Fish in all aggregations ate a variety of sizes of juvenile-adult euphausiids (*Thysannoessa raschii* and unidentifiable euphausiids) and amphipods (*Themisto pacifica*, *Primno macropa* and *Hyperia* sp.). Even though the allopatric fish presumably expended more energy to consume the high numbers of small prey that constituted more prey biomass than the sympatric pollock, they were in better condition than the sympatric pollock. Nonetheless, the smaller sympatric pollock were not less inclined to prey on the energetically advantageous prey than sympatric herring; both species had low feeding measures and ate similar proportions of euphausiids. Given the apparent differences in euphausiid availability, continued predation on euphausiids by pollock and herring in areas where they were not collected suggests strong selectivity for this taxon. Euphausiids could have been consumed at night near the surface or during the day near the bottom (Krieger, 1985; Pearcy et. al, 1979). Also, the larger autumn fish may be better able to prey on late stage euphausiids than the smaller summer fish (Merati and Brodeur, 1996; Kamba, 1977; Haegele, 1997). Whether the differences in diet between fish in allopatric and sympatric aggregations are due to regional spatial differences in prey available, to time of day and depth, or to the species composition of the foraging aggregation remains unclear.

If competition occurs between sympatric species, one would expect that, given similar prey fields, the quantity or quality of prey consumed would improve when fish are allopatric compared to when they are sympatric. Spatial variation in diet of YOY herring from four bays in PWS (Foy et. al, 1998) and for YOY pollock in three areas of the western Gulf of Alaska (Merati and Brodeur, 1996) have been reported previously. Our small sample sizes make it difficult to distinguish between diet characteristics that may relate to aggregation type (allopatric/sympatric) versus time of day, habitat, or region. The allopatric and sympatric herring in early autumn and the allopatric and sympatric pollock in late autumn consumed different proportions of the same taxa. Allopatric and sympatric fish may exhibit different behaviors that affect their distributions and therefore affect predation on euphausiids or other strong migrators. They might also partition the available prey to avoid competition, but our finding that less quantity of food was eaten by sympatric fish compared to allopatric fish suggests that competition was occurring. Alternatively, the sympatric herring and pollock could have had less full stomachs than the allopatric fish because of sampling time, if they had not been feeding actively near the surface where food was more abundant long enough to fill their stomachs.

We found high intraspecific diet overlap between allopatric and sympatric fish for both herring and pollock in autumn. Lack of intraspecific comparisons of allopatric and sympatric fish in each season is unfortunate, however, since differences in prey composition and the lower overlap observed between sympatric pollock and herring in October compared to November suggests that some prey partitioning does occur when resources are sufficiently abundant. Stomachs of sympatric pollock contained less food and fish were in poorer condition compared to allopatric pollock in late autumn, but these differences were not found for early autumn herring. These findings suggest that a combination of interference competition and seasonal or diel prey declines occurred. In another study, compared to allopatric herring, herring sympatric with sandlance that had similar diets shifted prey and ate less food, but they also shifted prey and ate less when sympatric with pink salmon that had different diets; these diet shifts and declines in food consumption were attributed to prey partitioning, predator size, and possibly to lower prey density (Sturdevant et. al, 1999). Boldt (1997) analyzed a subset of the pollock data included here, and speculated that differences in summer diet between pollock at different stations in central PWS might relate to differences in fish density that could lead to intraspecific competition, since pollock density was lowest at the only station of five where fish consumed large calanoids. However, we did not observe a clear pattern linking selection of any prey to lower fish density.

Although we could detect few differences in the quality of prey selected by fish in allopatric and sympatric aggregations, we did find differences in the quantity consumed by the two species. Trends toward decreased feeding from summer to late autumn were stronger for herring than for pollock, despite the fact that the early autumn and late autumn fish were not from the same cohorts. For herring, all feeding attributes declined from summer to late autumn. For pollock, fewer feeding declines were observed, and only for late autumn relative to summer. By late autumn, interspecific differences were also observed: proportionally fewer herring were feeding than pollock. Reduced total feeding and prey diversity, as well as increased diet overlap, could reflect declines in the numbers and types of prey available and a constriction in feeding for all fish. These factors could also indicate a density dependent convergence of the diets. Unfortunately, we have no zooplankton data for late autumn, but others have shown a steady decline in zooplankton biomass and macrozooplankters over the winter (Foy and Paul, 1999) or longer time scales (Tanasichuk, 1998a and b). In British Columbia during several years that encompassed the period of our study, adult abundance of *Thysanoessa spinifera* declined steadily due to warmer than usual conditions (Tanasichuk, 1998a), while production of *Euphausia pacifica* was higher in years of strong upwelling (Tanasichuk, 1998b). If the environmental changes in the Gulf of Alaska that have resulted in forage fish population shifts have also affected prey taxa such as euphausiids, then the trophic relationships and energy flows in PWS could be drastically altered. Unfortunately, long-term population data do not exist for most of these trophic levels.

Some of our results suggest that the seasonal decline in feeding occurs at the same time that total zooplankton in early autumn declines from summer high values. We estimated zooplankton densities in summer and early autumn of approximately 1.2 - 1.4 organisms per liter using different nets. However, results of our summer mesh trials suggested that zooplankton

abundance estimates would have been greater had we used the same small-mesh net employed in autumn; if so, trends toward more intensive feeding in summer were supported by a food supply of small calanoids that was 4x greater than in early autumn that year, and was similar to densities measured the next summer with the small-mesh net (Sturdevant and Hulbert, 1999). Nonetheless, a decline in zooplankton density from summer to autumn does not change our conclusions because the fish switched away from small calanoids to larger prey which were not differentially selected by the two plankton nets. Even if our density estimates are not directly comparable between summer and autumn, our finding that the percentage composition of the zooplankton did not vary with mesh size allows valid comparisons of seasonal prey selection, since the selection index we used is calculated with percentages.

The similarity of dietary requirements between YOY pollock and herring could induce competition when these fish co-occur during periods or in places of low food availability, such as late autumn-winter. Seasonal movement of juvenile pollock and herring into small bays may maximize food resources at the same time it induces density dependent interactions, because stormy conditions and spring tides that mix different water masses may concentrate the prey remaining in autumn, such as larvaceans (Alldredge, 1982). We found significant diet overlap based on either numbers or biomass of prey in both the summer and autumn, even though these species may occur sympatrically only in the autumn. Significant overlap values were also calculated by Willette et. al. (1997), who found that diet composition and the degree of diet overlap changed over a 24-hour diel sampling event in late summer. Diets of pollock and herring from sympatric sites also overlapped by more than two times the diets of fish at allopatric sites (Willette et. al, 1997).

Other evidence suggests that seasonal changes in prey availability affect feeding and diet more than sympatry does. Willette et. al (1997) found highly similar diets between juvenile pollock and herring in late summer in PWS, based on small calanoids, including *Pseudocalanus* spp., and malacostracan prey. In October, we observed fewer non-feeders and guts that were more full than in November. Furthermore, diet overlap was considerably lower among the sympatric aggregations of pollock and herring from early autumn than those from late autumn. This low overlap resulted from the early autumn sympatric pollock being more selective of large calanoids and eating proportionally more euphausiids, while the herring selected larvaceans. A diversity of available prey enhances the likelihood of partitioning between species, decreasing diet overlap. In late autumn, euphausiids were prominent in the diets of both species in sympatric aggregations, more so than in the early autumn diets. Decreased density and diversity of prey increases the potential for diet overlap.

Although the diets of allopatric pollock and herring in our study overlapped extensively in summer, the vertical distributions of these species did not overlap, at least during the day. The summer pollock were captured in deep water ($\geq 60\text{m}$) during the day, when we expected less active feeding than for autumn fish captured nearer the surface (15-20 m depth) at night, but just as much food quantity was consumed. Similarly, the summer herring caught at the surface during the day consumed just as much prey as the early autumn herring caught slightly deeper at night.

Similar prey could have been consumed by the two species at different times. Even if their vertical distributions did overlap at night (we had too few night samples to compare), having different principal times of day for feeding could result in highly similar diets without suggesting direct competition, since predation on the same prey resources would be temporally separated. Different feeding periodicities could result in indirect competition if prey resources are limited, however.

These feeding contrasts suggest that the two species' diel rhythms change between seasons or that they feed throughout the day. Our comparisons of day-night condition of prey also suggest that daily time of peak feeding could differ for the two species. Digestion indices indicated that pollock fed principally at night, while herring apparently fed principally during the day. Diel studies reported similar patterns of feeding for pollock (Merati and Brodeur, 1996; Brodeur and Wilson, 1996) and herring (Willette et. al, 1997; Blaxter and Hunter, 1982; DeSilva, 1972). Therefore, some of the seasonal differences in feeding we have demonstrated may actually be diel differences. However, they do not explain the lack of differences between summer and early autumn feeding for both species or the existence of differences between early autumn and late autumn feeding for herring. Similarly, since the autumn allopatric samples were collected earlier in the day than the sympatric samples, the fact that allopatric pollock stomachs were more full than sympatric stomachs in late autumn might be related to feeding time rather than trophic interactions such as interference competition, particularly since euphausiids (prey with a strong DVM pattern) were a smaller proportion of the diet by number and biomass. However, the fact that allopatric herring stomachs were no more full than sympatric stomachs in early autumn at a time of day when the state of digestion indicates that they should have been feeding more suggests that a factor other than sympatry is involved. Unfortunately, our samples were not extensive enough to demonstrate a seasonal diel feeding or depth-related pattern that might occur with a changing light regime and our allopatric-sympatric comparisons are based on small sample sizes. However, Krieger (1985) speculated that YOY pollock switch from feeding principally during the day in summer to feeding at night in autumn based on a change in digestion of prey with time of day.

Trends toward greater size in late autumn were stronger for pollock than for herring. Both pollock and herring were larger in early autumn than in summer, but only pollock were larger in late autumn than in early autumn. Pollock also appeared to be in better condition than herring, since only their weight increased from early to late autumn. Such growth is advantageous for survival through the extreme conditions of coming winter. Juvenile pollock tested between the temperatures of 3° C to 7.5° C exhibited a linear increase in consumption (%BW/day) with temperature, but grew more rapidly at colder temperatures under conditions of low food. The maintenance ration for these fish was also lower at the colder temperature (Smith et. al, 1986). The pollock in our study consumed well above this maintenance ration in all seasons, but the low prey %BW of herring in late autumn could indicate starvation.

For pollock, the larger size in November compared to October, along with the smaller size of sympatric fish compared to allopatric fish in November, suggests that pollock continue to feed

in late autumn but could be at a competitive disadvantage when they co-occur with herring. For herring, the similar size of both allopatric and sympatric fish in October along with unchanged sympatric size in November suggests that seasonal feeding declines are more important than sympatry. These species may have different strategies for overwintering, as suggested by differences reported for feeding success. Among YOY herring, the proportion of empty stomachs peaked in December (Foy and Paul, 1999), but among YOY pollock, no empty stomachs were observed in any period (Krieger, 1985). In terms of avian predation, not only was there a major difference in the nutritional quality between these fish species--pollock lipid content was low compared to herring--but lipid content also varied in opposite directions with age (Anthony and Roby, 1997). Herring lipid content increased with age and pollock lipid content decreased with age. Therefore, the feeding differences we observed support the ideas that herring are dependent on stored energy to survive, while pollock allocate energy from year round feeding for somatic growth.

The larger size of the November pollock should have been accompanied by consumption of greater prey biomass compared to the smaller October pollock, but only the allopatric pollock ate more. Sympatric pollock were larger but did not consume more prey. We observed decreases in prey numbers from early to late autumn that are compatible with changes from small to larger prey of similar caloric density. However, the seasonal increase in predation on large prey by both species did not coincide with size increases for both species. Only the late autumn pollock were larger than their early autumn conspecifics. A size no larger among late autumn herring than either early autumn herring group is consistent with our finding that they fed less in late autumn than in early autumn, but larger size of the pollock is not consistent with our finding that these fish also fed less in late autumn than in early autumn. Herring were apparently affected by diminished prey resources sooner than pollock were. If herring do enter the winter lagging even a month behind pollock in the accumulation of winter energy stores, the edge gained by pollock could enhance their potential to supplant herring in PWS. However, our findings could relate to interannual differences instead of seasonal differences. Regardless of the source of the differences, the pattern for pollock differs from the pattern for herring. Foy and Paul (1999) found that herring whole body energy content increased from October to November, then declined through the winter. A steady decline in zooplankton biomass between the months of October and February in their study coincided with feeding decline and reliance on stored energy. Krieger (1985) observed pollock feeding throughout the year, with stomach fullness highest in July (100%) and lowest in December (50%). He also observed declining feeding rates in October compared to August and September, not only in terms of stomachs fullness, but in relation to prey numbers because of the switch from small prey to larger prey.

One explanation for the continued growth of pollock in late autumn is lower energetic requirements. Energy can be conserved during times of reduced prey by altering behaviors to decrease metabolic costs, such as restricting movement or residing in regions of colder ambient temperature, for example deeper water (Sogard and Olla, 1996). If environmental temperatures drop after October in PWS, growth could continue under lower food conditions (Smith and Paul, 1986). Although it is reasonable to assume that zooplankton becomes less available during this

period of transition to winter, we do not have zooplankton data from November, 1994 to compare availability of the numerically prominent prey in the diets at that time, large calanoids and larvaceans.

The seasonal distributions of YOY pollock and herring are partially determined by adult life history traits. Herring spawn nearshore, inter- and subtidally; their adhesive eggs are retained upon algae and benthic structure. After hatching and through the juvenile stage, larval herring may be transported away from spawning areas or may remain in the nearshore bays (Lassuy, 1989; Stokesbury et al., 1998). The onset of schooling behavior occurs at metamorphosis at 25-40 mm, at approximately 10 weeks of age (Lassuy, 1989; Gallego and Heath, 1994). In contrast, pollock broadcast spawn their eggs in deep water offshore (Smith, 1981); the demersal eggs may be carried throughout PWS by advective currents. Pollock larvae may hatch in a nearshore retention area or in the more open areas of the sound, and therefore be exposed to different rates of predation, cannibalism and advection. Large numbers of YOY pollock have been observed in nearshore bays, which may be important nursery areas (Smith et al., 1984; Brodeur and Wilson, 1996; Wilson, 1997).

For sympatry to occur, the distribution of juvenile walleye pollock and Pacific herring must overlap in three dimensions: time (seasonal and diel), and both horizontal and vertical space. Since both species' patterns of movement change ontogenetically in each of these dimensions, their behaviors suggest that utilization of similar habitats could occur at different times and the degree of spatial overlap is likely to vary. In general, juvenile herring school near the bottom along shore during the day, then move up to the surface at dusk and disperse (Blaxter and Hunter, 1982; Lassuy, 1989; Haegele, 1997). Early YOY pollock stayed principally in surface water above the thermocline, performed a DVM, and dispersed or moved inshore at night; depth distribution increased from summer to autumn (Bailey, 1989; Brodeur and Wilson, 1996; Olla et al, 1996). In Auke Bay in southeastern Alaska, demersal YOY pollock inhabited nearshore waters beginning in July, remaining until October at a size of 92 mm. These nearshore juvenile pollock were caught in summer at 10-20 m depths during the day, in early autumn at 10-40 m depths mainly during the day, but in late autumn at 40-60 m depths (near bottom) mainly at night (Krieger, 1985). Observations of YOY pollock at some of these same sites in Auke Bay were consistently made over 22 years of diving, confirming non-random habitat utilization (Carlson, 1995). Herring and pollock in PWS were depth stratified in July, October, and March, with herring occupying the upper 30 m of the water column and pollock associated with the bottom (Stokesbury et al., 1998). Both species aggregated in bays in July and October, with herring in tighter schools than pollock. Perhaps summer growth allows both species to reach an early autumn size great enough to promote volitional migration into common nearshore areas. The summer-autumn difference of 30-40 mm in mean FL that we observed in both pollock and herring could serve this function. Some authors have suggested the two species simply have an affinity for the same habitats, rather than a strong species association (Brodeur and Wilson, 1996). Yet at least some of the population occurs sympatrically in summer and autumn (Haldorson et. al, 1996; Willette et. al, 1997). Sympatry may be limited in spring and early summer because of different hatching habitats, time to metamorphosis, and differential rates or timing of migration into

common areas. Unpublished seasonal data from SEA, 1994 (M. Willette, pers. comm.) showed that, of the monthly sets catching herring or pollock from April to September, after May, > 50% of herring sets also caught pollock, and after July, > 50% of pollock sets also caught herring. This pattern suggests that sympatry increases seasonally, with highest rates of co-occurrence in the autumn. However, fishing gear and duration of the tows are unknown components that may mask any micro-scale spatial segregation of the species.

Pollock migration follows both diel and ontogenetic rhythms on horizontal, vertical and seasonal scales (Brodeur and Wilson, 1996). In the laboratory, Pacific herring feeding response decreased in October-November through February-March, when they again began to put on fat and condition (Stacy and Houston, 1982, in Lassuy, 1989). In this study, surface temperatures where fish were located were lower in late autumn than in early autumn. Surface temperatures were approximately 12°C in summer, 10°C in early autumn, and 7-8°C in late autumn (Boldt, 1997). The thermocline, when present, tended to be slightly deeper in late autumn, progressing from 40-50 m in July-August to 50-60 m in November; temperatures below the thermocline remained at 5-6°C in each season. The vertical distribution of YOY pollock and herring coincided with the temperature maximum in November (Haldorson, 1995). If this pattern of water column conditions is typical, then movement from cool, deeper offshore locations in summer to shallow water in bays in autumn achieved little change in the temperature quality of habitat occupied between summer and autumn. Differences in other qualities may be more important. For example, food production may continue later into the autumn in bays that are warmer and more nutrient-rich than offshore, or the little food produced late in the year may be concentrated in bays by hydrographic features. In July and October, surface waters of PWS bays were colder than outside the bays; the pattern reversed in March (Stokesbury et. al, 1998). In combination with better feeding conditions and favorable hydrographic conditions, movement into the bays by autumn could prolong seasonal feeding. } }

It is clear from acoustic estimates of biomass that pollock and herring populations vary interannually and seasonally. In a review of the distributions and species associations of pollock in NMFS historical bottom trawl surveys in the Gulf of Alaska, Shima et al (1996) reported a lower association of YOY pollock with herring after 1980. In contrast to 1995, the APEX July, 1996 surveys caught only two sets of YOY pollock sympatric with other species; they were seined nearshore and were sympatric with species other than herring (Haldorson et al., 1997; Sturdevant et al., 1999). This fits in with the timing of inshore movement documented by Krieger (1985). The APEX project has shown that pollock and herring frequently associate with other species (Haldorson 1995, 1996, 1997).

It seems clear that, with an affinity for similar habitats and similar food requirements, juvenile pollock and herring distributions will overlap. If schools are less tightly aggregated during food searching, which expands the total volume occupied while decreasing competition between individuals, two schools have a greater tendency to overlap. YOY pollock forage in socially interactive groups when food occurs in ephemeral patches (Ryer and Olla, 1992; 1995) and the activity of feeding in schools attracts other fish. With dispersed food, they ignore others'

behavior and feed more independently, but may be more aggressive toward intruders. Hunger stimulated increasingly active searches for food. Laboratory studies also showed that smaller individuals formed less cohesive schools and were less active than larger individuals. More studies comparing the spatial and temporal patterns of distribution are needed to clarify the extent and frequency of YOY pollock and herring interactions in Prince William Sound and elsewhere.

The potential for food competition between pollock and herring appears to be greater in the autumn, particularly late autumn, than in the summer. Clearly, both pollock and herring consumed the same types of food in different proportions in each season, whether allopatric or sympatric. Although their diets are very similar in all three seasons, the synergistic effects of increased rates of sympatry and declining zooplankton stocks in autumn may cause both feeding declines for these species and higher diet overlap between them in late autumn. This occurs at the same time that approaching winter hydrography creates more metabolically demanding conditions. Previous studies have shown that stored energy is used extensively by herring of all ages to survive the winter; autumn may be the most important for YOY herring, which frequently had too little fat stored to persist through lean times (Paul, 1997; Paul et. al, 1998; Paul and Paul, 1998; Foy and Paul, 1999). Large-scale changes in the environment, such as ENSO events which cause changes in water temperatures and current patterns, may have greater effects on some fish populations than dramatic, one-time events such as the *Exxon Valdez* oil spill. If walleye pollock have a competitive advantage over Pacific herring in the critical autumn period, dramatic negative effects on the PWS marine bird and mammal populations which rely on these forage fish resources could occur. However, increasing numbers of another energy-dense forage species, the sandlance *Ammodytes hexapterus*, have been reported in PWS recently (Brown et al., 1997??; Kuletz et al.??). The trophic interactions between sandlance and walleye pollock, if any exist, are unknown. Additional and changing species interactions are likely to occur with such community changes, and result in unknown ecosystem impacts. Therefore, long-term monitoring is essential to improve understanding of the PWS ecosystem. Continued studies in PWS will expand our understanding of interactions between pollock, herring, and other forage species.

Acknowledgments - Chapter 2

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